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SOME ASPECTS OF RESEARCH IN PHYSIOLOGY, NEUROPHYSIOLOGY AND NEUROANATOMY AT THE UNIVERSITY OF OSLO, NORWAY

by

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10 January 1966

SOME ASPECTS OF RESEARCH IN PHYSIOLOGY, NEUROPHYSIOLOGY AND NEUROANATOMY AT THE UNIVERSITY OF OSLO, NORWAY

The Institutes of Physiology and Anatomy, and the Neurophysiology Laboratory, are located in the old University center in Oslo, a few blocks from the bustling and attractive center of the city. Most of the other divisions of the University, which now has some 10,000 students, are located at a new, ultramodern campus on the outskirts of the city. It is expected that the medical institutes will be located there in about five years.

It is not the intent of this report to summarize superficially the research programs of all members of each of these institutes. Rather, it is my purpose to report in some detail certain areas of research by one or more individuals which, in my opinion, represent significant contributions.

THE INSTITUTE OF PHYSIOLOGY

The Institute of physiology is under the direction of a new Head, Prof. Bjarne A. Waaler. Waaler is an extremely energetic and bright young man, who is capable of establishing a productive group, provided the necessary support is received. He has worked in the past with I. de Burgh Daly in London. He is keenly interested in the teaching of medical physiology, and some of the problems and ideas with which he and other European physiologists are concerned will be the subject of a later report. Waaler has been Head of the Institute of Physiology for about two years, and now has several research projects in operation. He is still handicapped by a lack of adequate funds, but the situation is improving steadily. The research equipment of the Institute is relatively outdated, most recording still being done by kymograph. However, a new four-channel recorder is now in use.

The professional staff of the Institute of Physiology consists of Waaler (Professor), Leif Erikson (Associate Professor), Johan Steen, Egil Amundsen and Yngve Løyning (Established Research Workers), two scientific assistants and four research fellows, two of whom are supported by the Norwegian Research Council. The primary areas of research include projects on hemoglobin synthesis, plasma kinins, gas exchange in fishes, and pulmonary circulation.

Waaler has recently begun work on pulmonary blood flow in an isolated, perfused rabbit lung preparation. He is recording pulmonary artery pressure, ventilation and lung weight with fairly crude techniques, but ones adequate to yield the necessary data. This project is now being converted for recording with a

four-channel direct ink-writer, which should provide both more precise measurements and the capability of adding other parameters of measurement. This work has reached the stage where a first manuscript is in preparation. The isolated lung is perfused at a constant, non-pulsatile pressure. After a variable period of time, a significant increase in pulmonary artery pressure occurs spontaneously, indicating an intense vasoconstriction. During this time no significant change occurs in ventilation. This vasoconstriction is reversed completely by tri-cresol, which appears to inhibit ATP specifically. Vasoconstriction produced by a variety of pulmonary constrictor drugs including norepinephrine and several polypeptides is not affected by administration of tri-cresol. This research, which is in its incipient stages, requires considerable expansion. The observed fact of this remarkable specificity of tri-cresol in inhibiting a spontaneously occurring pulmonary vasoconstriction is of great interest and potential value. However, much remains to be done concerning the nature of the spontaneous constriction in this kind of preparation and concerning the mechanism of action of tri-cresol in reversing this constriction. To my knowledge there has not been any attempt to assess the histological status of the isolated lung preparation after varying periods of perfusion. This information should be obtained as well as studies on alveolar gas exchange, etc.

In a previous report it was demonstrated that certain polypeptides (bradykinin, kallidin and eledoison) all produce pulmonary vasoconstriction in an isolated rabbit lung preparation. Bradykinin was effective in doses as low as 1-5 micrograms, and was more potent, on a molar basis, than 5-hydroxytryptamine or norepinephrine. Kallidin was 30-50% more effective in producing vasoconstriction than was bradykinin, and eledoisin was strikingly more powerful than either of the other two polypeptides, causing marked pulmonary vasoconstriction in doses smaller than .001 micrograms. Responses to polypeptide injection were not affected by doses of Regitine which completely blocked vasoconstrictor responses to norepinephrine, nor by methysergide which was effective in blocking the response to 5-hydroxytryptamine. This evidence suggests that the mechanism of action of polypeptides in producing pulmonary vasoconstriction does not operate by way of liberation of catecholamines or 5-hydroxytryptamine.

A great deal of research effort in the Institute of Physiology is concerned with studies on plasma kinins and intestinal obstruction -- areas which I am not competent to assess critically. It might be useful, however, to list some recent publications in these fields from the Institute of Physiology:

Amundsen, E. and Gustafsson, B.E. Results of experimental intestinal strangulation obstruction in germ-free rats. J. Exp. Med. 117, 823-33 (1963).

Amundsen, E. and Midtvedt, T. The toxicity of fluid from experimentally strangulated intestinal loops in the rat. J. Surg. Res. 4, 306-13 (1964).

Hauge, A., Amundsen, E. and Waaler, B.A. Changes in blood proaccelerin (Factor V) in rats with intestinal strangulation obstruction. Thromb. et Diath Haemmor. 12, 49-63 (1964).

Amundsen, E., Waaler, B.A., Dedichen, J., Laland, P., Laland, S., and Thorsdalen, N. Kinase inhibition by a fluorescent substance prepared from liver. Nature 203, 1245-48 (1964).

Amundsen, E. and Nustad, K. Kinin-forming and destroying activities of saliva. Brit. J. Pharm. & Chemotherapy 23, 440-44 (1964).

Amundsen, E. and Rugstad, H.E. Influence of some pathogenic bacteria on kinin formation and destruction. Brit. J. Pharm. & Chemotherapy 25, 67-73 (1965).

Amundsen, E. and Nustad, K. Kinin-forming and destroying activities of cell homogenates. J. Physiol. 179, 479-88 (1965).

With the addition of Dr. Johan B. Steen to the Institute, a new area of research has been instituted. Steen has been working in a field best covered by the term "comparative physiology," including studies on oxygen exchange in small aquatic animals with a modified Scholander respirometer, thermoregulation in birds and gas exchange in fish. Together with I. Steen, he published an interesting paper in Acta physiol. scand. 63, 285-91 (1965), entitled, "The Importance of the Legs in the Thermoregulation of Birds." In studies on herons and gulls it was shown that the entire heat production of the bird could be lost through the legs at high environmental air temperatures (35°C). At 20°C, about one-half the total heat production could be dissipated from the legs. Heat loss from the legs to water was found to be about fourfold that from the legs to air. The physiological mechanism responsible for controlling the rate of heat dissipation from the legs (presumably vascular control) responds rapidly to sudden changes in environmental air temperature. This was studied by measuring the water temperature surrounding one leg of a heron while the environmental temperature was rapidly lowered from 35°C to 5°C. During the control period at an air temperature of 35°C, water temperature surrounding the leg increased linearly at a rate of about 0.18°C/min. Thirty seconds after a rapid decrease in environmental

temperature, heat loss from the leg into the surrounding water had decreased markedly to the point where the change in water temperature was only 0.03°C/minute. Although the authors made no measurement of hypothalamic temperatures, it was felt that the rapidity of this response indicated a reflex initiated by peripheral receptors. The vascular arrangements of the leg in many birds provide the possibility of countercurrent heat exchange, as well as shunts that can permit a bypass flow of blood around the retia. It would be of great interest if Steen would investigate the nervous control of these blood vessels as an extension of this work.

THE NEUROPHYSIOLOGICAL LABORATORY

This laboratory, which is extremely active in research, operates essentially as a fully independent department. It is directed by Prof. Birger Kaada, who has made oustanding contributions in the field of CNS control of autonomic function and various aspects of behavioral neurophysiology, especially as related to the limbic system. Kaada has spent considerable time in the United States, working with Pribram and with John Fulton at Yale. He has also worked at various times with Jasper in Montreal and Granit in Stockholm. The Neurophysiological Laboratory is presently located in diffuse quarters in the Anatomical Institute. There is a shortage of adequate space, but an obviously maximal use of what is available. Within a few months the Neurophysiological Laboratory will move into larger quarters in the Institute of Physiology.

The department is well equipped with much of the electronic instrumentation that is so necessary in modern neurophysiological research. However, certain of the research problems under investigation have reached a stage where a new generation in electronic instrumentation is required. This will essentially involve computers, and will raise problems for the department in obtaining the sizeable funds involved. The research funds available to the Neurophysiological Laboratory have grown steadily in Kaada's 15-year tenure. In recent years research support has been provided by the following sources:

1. The Norwegian Research Council for Science and the Humanities
2. The Norwegian Council on Cardiovascular Diseases
3. The Anders Jahres Foundation
4. The Fridtjof Nansen Foundation
5. United States Public Health Service, National Institutes of Health

6. The Rockefeller Foundation

7. European Office, Air Research and Development

8. The Wellcome Trust, London .

The permanent staff consists of Prof. Birger Kaada and Drs. Jan Jansen, Jr., Per Andersen and Holger Ursin. Andersen has had two years in Eccles' laboratory in Australia (1961-63), from which a remarkable series of excellent publications was derived. Ursin was in the United States during 1962-64, spending 18 months at the University of Chicago, two months at Michigan and three months at NIH. In addition to the permanent staff there are 13 research fellows working in the Neurophysiological Laboratory, as well as several foreign guests.

The research activities of this department can be roughly grouped into six areas:

A. Autonomic nervous system - Endocrinology

B. Control of movement

C. Sleep mechanisms - Reticular formation

D. Behavioral studies in animals

E. Muscle and nerve

F. Physiology of synapses

The current status of research in some of these areas is reviewed below.

A. Autonomic nervous system - Endocrinology

The primary interest in recent years has been the influence of the autonomic nervous system on uterine motility in estrogenized rabbits, and on the responses of the urinary bladder in cats.

1. Uterine Motility

Rapid distention of the myometrium produces a quick contraction followed by increased rhythmic activity, the frequency of which is increased with the degree of distention. This pacemaker activity is directly related to the tension in the myometrium. The myogenic nature of this response to distention is indicated by the lack of effect of autonomic blocking

drugs and local or spinal anesthesia, as well as the independence of the two uterine horns in response to distention. Stimulation of the hypogastric nerve produces maximal uterine contraction at a frequency of 30-50 cps. Stimulation for only a few seconds results in a single contraction, whereas prolonged stimulation at low frequency results in a series of rhythmic contractions. Evidence has been gathered which demonstrates the presence of adrenergic fibers in the hypogastric supply to the myometrium. Similar evidence for the presence of cholinergic fibers is lacking. Splanchnic nerve stimulation produces qualitatively similar responses, but of longer latency and more gradual onset.

It has been proposed by these workers that the sympathetic nervous system exerts a tonic influence on the uterus. It has been demonstrated that a variety of sensory inputs can influence uterine motility, e.g., stimulation of the rectum, and electrical stimulation of various visceral and somatic afferent nerves. In addition, similar responses in uterine motility can be obtained from asphyxia and carotid artery occlusion. Responses to all of these stimuli appear to be the result of sympatho-adrenal activation, the effector action being an initial uterine contraction followed by a period of decreased rhythmic activity. This effector response is eliminated by sympathetic blocking agents, as is the inhibition of "spontaneous" rhythmic contractions produced by stimulation of the depressor nerve. The latter response presumably is mediated by a sympathoinhibitory reflex.

Various parts of the brain were explored in order to map those areas which influenced uterine motility. In the medulla, excitatory responses were elicited from the lateral part, and inhibitory responses from the midline region. This distribution is similar to the general pattern of sympathetic influences of the medulla on other autonomic effectors such as the blood vessels. Stimulation of the periformical, dorsal, lateral and posterior hypothalamus produced excitatory responses. Excitation of uterine motility was also elicited by stimulation of the ventromedial hypothalamus, but this was due to oxytocin release. Inhibition was observed when a restricted area of the lateral hypothalamus was stimulated. Finally, excitatory responses were also derived from the sensorimotor cortex, anterior limbic region and amygdala. Several cortical areas produced inhibition of uterine motility, including the sensorimotor cortex and orbital surface.

2. Urinary bladder motility

Studies have been carried out to determine whether there are antagonistic effects between sympathetic and parasympathetic nerves to the urinary bladder. Intravesicular pressure was recorded by direct cannulation of the bladder, leaving the urethral

outlet intact. In this preparation, bilateral section of the parasympathetic nerve supply results in abolition or reduction of rhythmic activity. Subsequent denervation of sympathetic fibers causes resumption of rhythmic contractions, although they are of smaller amplitude. Reversal of the sequence of denervations produces the expected findings, i.e., hyperactivity after sympathectomy of the bladder, followed by restoration of more normal contractions when the parasympathetic nerves are out. A similar study was performed to determine antagonistic influences of the autonomic innervation on micturition. Section of parasympathetic fibers abolished the micturition reflex, whereas primary sympathectomy reduced the threshold for micturition, thus demonstrating an inhibitory role of sympathetic nerve fibers on the micturition reflex. Finally, studies were carried out on supraspinal influences upon the induction or inhibition of micturition. In the latter case, micturition was induced by rapid filling of the bladder. Excitatory areas were found in the amygdala and pyriform cortex (corticomedial area), ventromedial hypothalamus, posterior cingulate gyrus and upper brain stem reticular formation. The excitatory response from all regions was eliminated by denervation of parasympathetic nerves to the bladder, but were unaltered by sympathectomy. Inhibitory responses from supraspinal areas were abolished by sympathetic denervation of the bladder.

B. Control of Movement

A number of experimental approaches are being made to problems dealing with muscle receptors and fusimotor activity in the cat, much of which cannot be reviewed here due to space limitations. However, a brief description can be presented of a very significant study on the response patterns of nerve fibers in the dorsal spinocerebellar tract. Three different types of units in second order neurons of the dorsal spinocerebellar tract have been identified during the response to muscle stretch. The response in single units of these second order neurons is very similar in general to that of the corresponding receptor in the muscle. Thus the cerebellum is provided with three distinct items of information about the mechanical status of the muscle: (1) a mixed signal of muscle length and rate of movement (Group Ia units); (2) a signal primarily of muscle length (Group II units); and (3) a signal related to the degree of contraction in the muscle (Group Ib units).

C. Sleep Mechanisms - Reticular Formation

It has been known that EEG synchronization and behavioral sleep can be produced in unanesthetized animals by low frequency

stimulation of the preoptic region, reticular formation, caudate and medial thalamus. Recent experiments at the Neurophysiological Laboratory in Oslo have shown that EEG synchronization and behavioral drowsiness can also be evoked by low frequency (6 cps) stimulation of the subcallosal cortex. It was not possible to induce deep sleep from this area and the effects were less marked than those from the preoptic region. It has been proposed that this cortical area is part of a descending "deactivating" and inhibitory system which acts on subcortical sleep-producing mechanisms.

In another series of experiments it has been shown that high frequency (200-300 cps) stimulation in the midbrain in lightly anesthetized cats may on occasion produce EEG synchronization, i.e., immediate and wide-spread increase in cortical slow wave activity. This response is not obtainable in unanesthetized animals, and the synchronization response shows higher threshold and finally disappears as the depth of anesthesia is increased. The response could be obtained from points in the entire midbrain reticular formation. An area of low threshold for this response was discovered in the lower midbrain at the decussation of the brachium conjunctivum. This area of low threshold, however, appears to be independent of the brachium conjunctivum, since the response was still present in chronic animals following removal of the cerebellum.

D. Behavior Studies in Animals

Several years ago Kaada and his associates demonstrated deficits in the performance of rats in maze learning following bilateral lesions in the hippocampus. Other workers have failed to observe this effect. Recent experiments by Kaada and associates have confirmed the original finding, and have also obtained evidence that the type of maze used to discriminate lesions is of great importance. In these experiments it was also found that different brain structures are involved in maze learning and in passive avoidance learning, since the latter was not affected by the hippocampal lesions.

Another series of experiments has been performed to study the effects of forebrain lesions on sex incentive. The criterion of sex incentive was the number of crossings of an electrified grid toward a rat of opposite sex. The number of crossings was significantly decreased by bilateral destruction of (1) upper portion of sensorimotor cortex; (2) amygdala; and (3) the olfactory bulb. Increased number of crossings were observed after bilateral lesions in (1) septal area; (2) temporal-insular cortex; and (3) stria medullaris and habenula. The decrease in incentive produced by any of the above lesions could be counteracted by bilateral lesions in any of the above-named areas which increased incentive. Other aspects of the animals' response and physiology

remained normal (spontaneous motor activity, sensitivity to the grid, estrous cycle, etc.).

THE ANATOMICAL INSTITUTE

This Institute is directed by Prof. Jan Jansen. I had hoped to spend considerable time talking with Prof. Alf Brodal about his neuroanatomical studies, but had to settle for a brief conversation. Brodal at present is serving a three-year term as Dean of the Faculty of Medicine, which has limited his time for research in the past few years.

Brodal has recently carried out experiments on the termination of primary vestibulocerebellar fibers in the cat. Sterile lesions of the vestibular nerve were made, and animals sacrificed from 5-19 days afterwards. Distribution of degenerating fibers was studied from brain sections treated by two silver impregnation methods, those of Nauta and of Glees. Primary degenerating fibers were found in the ipsilateral cerebellar cortex in the nodulus, flocculus, uvula, and ventral paraflocculus. There was also evidence of termination of some fibers in the dorsal paraflocculus, lingula and dentate nucleus. A few fibers distributed to the contralateral half of the cerebellum, reaching corresponding areas. There was no evidence, however, of a contribution of fibers from the vestibular nerve to the medial fastigial nucleus. These findings indicate that the functional "vestibulocerebellum" is not confined to the flocculonodular lobe. Moreover, there are morphological differences between these receiving areas as compared with the rest of the cerebellar cortex, which is contrary to the general view that this is uniformly structured throughout.

When his term as Dean of the Faculty of Medicine ends, Brodal expects to continue his work on vestibular and cerebellar structure. He is currently prepared to undertake a precise study using electron microscopy. The complexities of the nervous system and the huge number of structural elements involved make one admire the determination of Brodal to carry on his superb work at a new level of resolution. As he pointed out during our conversation, such an undertaking is only possible when one is thoroughly familiar in precise detail with the structure as seen under the light microscope. With his background and knowing precisely what he wishes to examine with electron microscopy, Brodal's first published reports in this field will be keenly anticipated.

For the past 15-20 years the reticular formation has been a subject of intensive investigation by neuroanatomists and neurophysiologists. It is an area to which Brodal has made

significant contributions. He has recently written a stimulating paper on the role of the reticular formation and other parts of the brain as related to consciousness. It is entitled "Anatomical Points of View on the Alleged Morphological Basis of Consciousness," and appeared in Acta Neurochirurgica 12, 166-86 (1964). Perhaps because his exposition struck such a responsive chord in my own feelings on this subject, I think it worth-while to summarize briefly the essence of his argument.

Anatomically the reticular formation can be divided into several cellular or nuclear groups. These groups differ both as to their connections and cytoarchitecture. The most common element of the reticular formation is not the associational cell but, rather, long axons projecting in caudal and/or rostral direction. Brodal points out that many of the receptors in the periphery give rise to specific fiber systems which do not send off collaterals to the reticular formation. This includes the medial lemniscus. He then questions the concept that the reticular formation works as an entity in the maintenance and level of consciousness. Finally, there is a discussion of the connections of the reticular formation with many other areas of the brain such as sensory cranial nuclei, periaqueductal gray, cerebral cortex, limbic system, etc., all of which may have a role in the process of consciousness. Brodal states the essence of his argument as follows: "We may indeed ask whether it is not timely to deprive the RF of some of its supremacy as concerns consciousness, and to consider this, like so many other functions, as being more or less dependent on the whole brain. It would perhaps help to clarify thoughts if we agreed to delete the word 'reticular' from the concept of the 'reticular ascending activating system'."

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13. ABSTRACT

Visits were made by author to the Institutes of Physiology and Anatomy and the Neurophysiology Laboratory, Univ. of Oslo, Norway, and this Tech. Report reports in detail certain research areas which are significant, e.g., Waaler's work on pulmonary blood flow in isolated, perfused rabbit lung preparation, and production of pulmonary vasoconstriction by certain polypeptides. Also discussed is Dr. J.B. Steen's work on thermoregulation in birds, gas exchange in fish. The Neurophysiological Lab's work on the autonomic nervous system (endocrinology) is reviewed, also control of movement, sleep mechanisms and reticular formation; behavioral studies in animals, including effects of forebrain lesions on sex incentive. The work of A. Brodal at the Anatomical Inst. on termination of primary vestibulocerebellar fibers in the cat is reviewed.

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